Comparative analysis of the 1980s and 2004 macrozooplankton composition and distribution in the vicinity of Kerguelen and Heard Islands: seasonal cycles and oceanographic forcing of long-term change

by

Brian P.V. HUNT* (1), Evgeny A. PAKHOMOV (1) & Richard WILLIAMS (2)

ABSTRACT. - In this paper we present historic macrozooplankton data from the vicinity of the Kerguelen Islands during the Ukrainian Skif and Kalper (SKALP) surveys in February, April and July-August of 1987 and February 1988, in addition to a monthly composite of seston data collected during *ad hoc* cruises between 1980 and 1990. We compare these data with more recent surveys conducted at Heard Island (February 2004) and the Prince Edward Islands (PEI) to the west of the Kerguelen Plateau (April 1997 and April 2003). A strong seasonal cycle of seston and macrozooplankton biomass was evident in the SKALP surveys, peaking between December and April. Kerguelen Plateau and PEI macrozooplankton were generally dominated by euphausiids, chaetognaths and amphipods, but salps were of major significance to the south of the PEI. Comparison of species composition at the Kerguelen Islands in 1987/1988 with Heard Island in 2004 lends biological support to recent estimates from satellite altimetry that the Polar Front has shifted from passing north of the Kerguelen Islands to passing south of Heard Island in 2003. As key food-web components, long-term changes and regional differences in macrozooplankton communities have significant implications for food web dynamics with respect to the type, quality and quantity of macrozooplankton prey available to top predators.

RÉSUMÉ. - Analyse comparative de la composition et de la distribution du macrozooplancton lors des années 1980 et en 2004 aux abord des îles Kerguelen et Heard : Cycles saisonniers et effets du changement à long terme du forçage océanographique.

Les données historiques sur le macrozooplancton du large des îles Kerguelen obtenues lors des campagnes de prospection Skif et Kalper (SKALP) réalisées en février, avril, juillet-août 1987 et février 1988, ainsi que des données mensuelles composites sur le seston obtenues lors de campagnes *ad hoc* menées entre 1980 et 1990, sont présentées dans cette contribution. Ces données sont comparées à des campagnes de prospection plus récentes autour de l'île Heard (février 2004) et des îles Prince Edward (PEI) (avril 1997 et 2003) situées à l'ouest du Plateau de Kerguelen. Un fort cycle saisonnier du seston et de la biomasse macrozooplanctonique a été mis en évidence lors des campagnes SKALP, atteignant un maximum entre décembre et avril. Le macrozooplancton du Plateau de Kerguelen et de PEI était généralement dominé par les euphausides, les chaetognathes et les amphipodes mais les salpes représentaient une importance substantielle au sud de PEI. La comparaison de la composition en espèces aux îles Kerguelen en 1987/1988 avec celle de l'île Heard en 2004 sert de support biologique aux récentes données d'altimétrie satellitaire qui estiment que le Front Polaire s'est déplacé du nord des îles Kerguelen au sud de l'île Heard en 2003. Les changements à long terme et les différences régionales dans les communautés macrozooplanctoniques, en tant que composantes clé des réseaux trophiques, ont des conséquences non négligeables dans la dynamique des réseaux trophiques selon le type, la qualité et la quantité de proies zooplanctoniques disponibles pour les prédateurs supérieurs

Key words. - Macrozooplankton - Kerguelen Island - Heard Island - Seasonality - Long-term change - Biogeography.

The Kerguelen Plateau is a vast submarine plateau with a meridional extent from 46ºS to 62ºS. The plateau comprises two parts, the northern Kerguelen plateau (NKP – 46 to 56ºS) and southern Kerguelen plateau (SKP – 57 to 62ºS), separated by the Fawn Trough (van Wijk *et al*., 2010). The plateau has two major island groups, the Kerguelen Archipelago in the northern NKP and the Heard Island and McDonald Island group in the southern NKP. Due to its meridional extent, the Kerguelen Plateau constitutes a major obstacle to the flow of the Antarctic Circumpolar Current (ACC) (Orsi *et al*., 1995; Belkin and Gordon, 1996). Topographic forcing and the shallow topography combine to bring iron and other nutrients to the surface over the plateau, creating conditions for consistently the largest seasonal phytoplankton bloom at any of the Southern Ocean island systems (Blain *et al*., 2007).

Oceanographically, it is generally accepted that the Sub-Antarctic Front (SAF) passes to the north of the NKP while the southern Boundary of the ACC passes to the south of the SKP (Orsi *et al*., 1995), however, there has been considerable debate over the location of the Polar Front (PF) in relation to the Kerguelen Plateau. Oceanographic data published up to the 1990's indicated that the Polar Front passed to the north of the NKP (Gamberoni *et al*., 1982; Orsi *et al*., 1995; Belkin and Gordon, 1996), while more recent works identify the PF as crossing the NKP immediately to the south of Kerguelen Island (Park *et al*., 2008a). Evidence has also been

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(1) Department of Earth and Ocean Sciences, University of British Columbia, Canada. [epakhomov@eos.ubc.ca]
(2) Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania, 7050, Australia. [Dick.Williams@aad.gov.au]
* Corresponding author [bhunt@eos.ubc.ca]

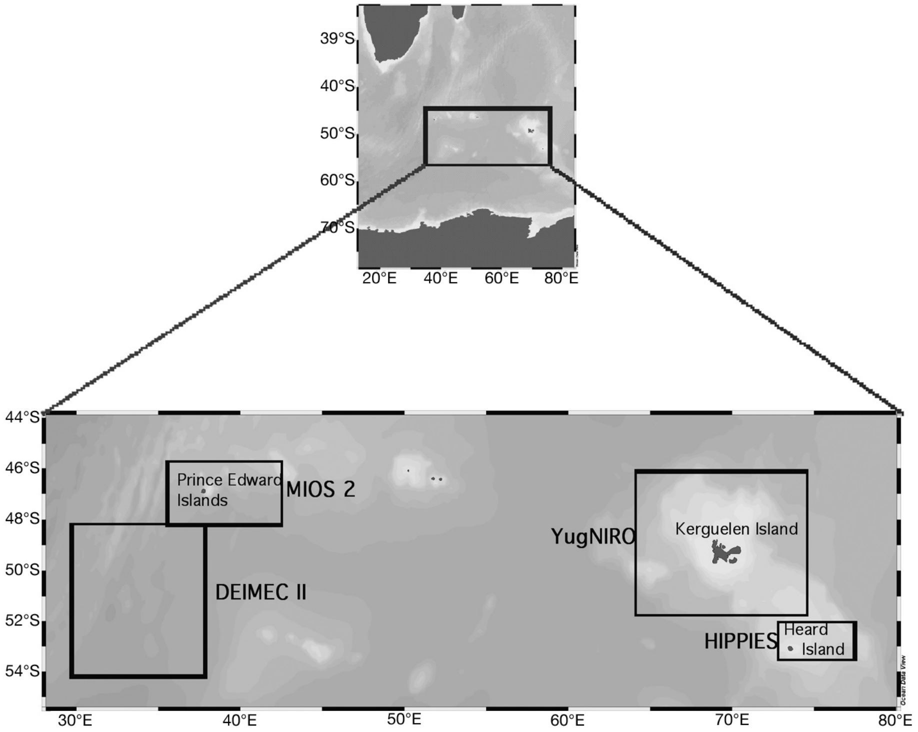


Figure 1. - Map showing the location of the sampling area and the regions sampled for macrozooplankton composition. The location of samples for the MIOS 2, DEIMEC II, YugNIRO and HIPPIES surveys are indicated.

found for the PF splitting into two jets west of the Kerguelen Plateau, designated as the surface and subsurface expression of the PF (Sparrow *et al.*, 1996). The subsurface front (N-PF), identified by the northern limit of the 2°C isotherm at 200 m, passed to the north of Kerguelen Island while the surface front (S-PF), identified as the maximum gradient of surface temperature between 2 and 6°C, passed south through the Fawn Trough.

The occurrence of two PF jets may account for some of the variability in the identified location of the PF. However, possibly of greater relevance is the observation from sea surface height anomalies that the N-PF passed north of the Kerguelen Islands between 1992 and 2003, but between 2004 and 2007 passed through the Fawn Trough, a southward shift of 10° latitude resulting from topographic deflection (Sokolov and Rintoul, 2009). Such an oceanographic shift is likely to have significant implications for primary production over the Kerguelen Plateau due to changes in hydrodynamics, e.g., upwelling or shelf water retention. Frontal zones in the Southern Ocean have steep physical gradients and separate regions of more uniform physical properties. These inter-frontal regions are typically characterised by distinct zooplankton communities, defined by different species composition and abundance levels of widespread taxa (e.g., Deacon, 1982; Gibbons *et al.*, 1997). Changes in the positions of frontal systems relative to the islands may therefore result in significant shifts in the composition of zooplankton across the Kerguelen Plateau.

Macrozooplankton is plankton typically larger than 20 mm in length, and comprise a diverse range of organisms, including crustaceans (e.g., euphausiids, amphipods, decapods), molluscs (pteropods and cephalopods), and gelatinous animals (e.g., chaetognaths, siphonophores, ctenophores, tunicates). As a group, macrozooplankton occupies a central position along the trophic pathway between primary producers and top predators, consuming primary production either directly as grazers (e.g., Tanimura *et al.*, 2008), or indirectly as predators of grazing mesozooplankton (e.g., Froneman *et al.*, 2002), and in turn are consumed by a multitude of top predators either directly or indirectly through their nekton predators (e.g., myctophids and squid) (Pakhomov *et al.*, 1996). In the Southern Ocean, macrozooplankton is in fact critical to the diets of vast numbers of vertebrate predators, including sea-birds, seals, and demersal and pelagic fish. This is epitomised at the Kerguelen Islands where the prey of the seabird and seal community has been estimated to comprise 55% crustaceans, 26% myctophid fish and 15% squid by mass (Guinet *et al.*, 1996). From data summarised for all Kerguelen sea birds, euphausiids alone averaged 13.3% of the diet, with a maximum of up to 80% (Cherel *et al.*, 2005). Although many vertebrate species forage in the productive neritic waters, the majority of prey biomass is harvested offshore. Despite the importance of the offshore community there have been few studies conducted in this part of the Kerguelen ecosystem.

In this paper, we present historical seston and macrozooplankton data collected in 1987 and 1988 during several joint Ukrainian (formerly USSR)/French expeditions to the region in the vicinity of the Kerguelen Islands onboard the YugNIRO [Southern Scientific Research Institute of Marine Fisheries and Oceanography (Kerch, Ukraine)] fishing vessels *Skif* and *Kalper* (SKALP expedition). These data provide a baseline for comparison with future macrozooplankton surveys in the vicinity of the Kerguelen Islands. In addition, we combine the YugNIRO macrozooplankton data with more recent macrozooplankton data collected from the vicinity of the Prince Edward Islands (1997 and 2003) by the South African National Antarctic Program (SANAP), and from Heard Island during the Heard Island Predator-Prey Investigation and Ecosystem Study (HIPPIES) expedition of the Australian Antarctic Division (Gales *et al.*, 2006). These combined data are used to assess macrozooplankton biogeography and evidence for long-term change over the Kerguelen Plateau in relation to the changing oceanographic environment.

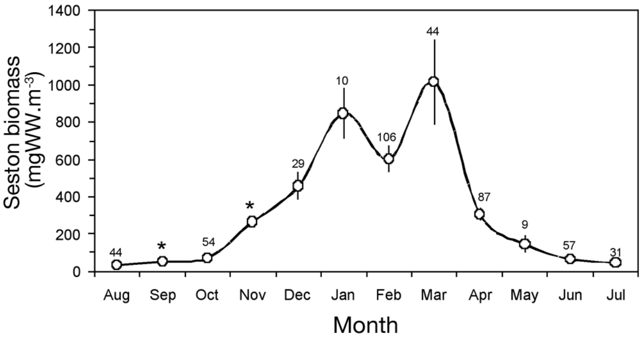


Figure 2. - Intra-annual variability (a composite of 1987 and 1988 samples) in the mean seston biomass in the 0-100 m layer in the vicinity of the Kerguelen Islands. Error bars show one standard deviation. Numbers correspond to number of stations sampled. *There were no surveys in September and November and the mean values are calculated by linear interpolation.

METHODS

An overview of the data sources used in this paper is presented in table I, and the methodologies used by each research program are outlined separately below.

SKALP surveys: 1987 to 1988

The SKALP surveys were designed to cover the shelf and slope of the Kerguelen Islands to sample the seston, mesozooplankton and macrozooplankton. We present the macrozooplankton and seston data here. Macrozooplankton samples were collected in three main seasons: summer (February 1987 and 1988), fall (April 1987) and winter (July-August 1987). All surveys had similar design, including eight radial transects starting at ~200 m isobath and ending at ~2000 m isobath, spaced 20 to 30 km apart. At each station, zooplankton was collected from standard depths, 0-50, 50-100, 100-200, 200-500 m (or to the bottom) using a modified Juday net (0.5 m^2, 150 μm mesh), fixed in 4% formaldehyde solution and sorted in the laboratory. For the purpose of this study we use the data for six macrozooplanton taxa, including three euphausiids, *Euphausia vallentini* Stebbing 1900, *Euphausia triacantha* Holt and Tattersall 1906, and *Thysanoessa* spp. (mostly *T. vicina*), one hyperiid, *Themisto gaudichaudii* Guérin-Méneville 1825, chaetognaths (*Sagitta* spp. and *Eukrohnia* spp.) and the tunicate *Salpa thompsoni* Foxton 1961. Densities are expressed as ind.m^{-2} over the entire water column sampled. The total mesozooplanton community, with the emphasis on copepods, is described by Semelkina (1993).

In addition, total seston was collected during numerous YugNIRO expeditions between 1980 and 1990 in the vicinity of the Kerguelen Islands (Tab. I). Sampling was conducted on an *ad-hoc* monthly basis with the exception of September and November. The data were then compiled as monthly composites irrespective of the sampling year. The number of stations sampled per month is illustrated in figure 2. Collections were made using a modified Juday net with 0.5 m^2 mouth area and equipped with 150 μm mesh. A standard depth of 0-100 m (or to the bottom if < 100 m) was sampled and the total biovolume of the seston was measured and expressed as mg WW (wet weight).m^{-3}. Volume filtered was

Table I. - Sampling details for all surveys used for this study, collected by YugNIRO, the South African National Antarctic Program (SANAP), and the Australian Antarctic Division (AAD). MK: Melnikov's net; RMT: Rectangular midwater trawl.

Region	Organization	Survey	Dates	Net	Samples (n)	Data type	Mesh	Depth (m)
Kerguelen Island	YugNIRO		Feb 1987 Apr 1987 July/Aug 1987 Feb 1988	0.5 m^2 Juday		meso / macro zooplankton	150 μm	500
Kerguelen Island	YugNIRO		Jan-Dec 1980/ 90 (*ad hoc* monthly sampling)	0.5 m^2 Juday		total seston	150 μm	100
Kerguelen Island	YugNIRO		Feb 1988	MK 0.22 m^2	44	macrozooplankton	0.5 mm	300
Prince Edward Is.	SANAP	MIOS 2	Apr 1997	RMT 8	20	macrozooplankton	4.5 mm	300
Prince Edward Is.	SANAP	DEIMEC II	Apr 2003	RMT 8	9	macrozooplankton	4.5 mm	300
Heard Island	AAD	HIPPIES	Jan 2004	RMT 8	21	macrozooplankton	2.5 mm	300

calculated using the mouth area and total distance travelled by the net assuming 100% filtration efficiency. During the summer (December to April), clogging probably occurred due to high phytoplankton biomass, and as a consequence, seston biomass may have been underestimated.

Finally, during February 1988 a Melnikov's net (mouth area 0.22 m^2, mesh size 0.5 mm) was used to collect macrozooplankton within the top 300 m. The net was towed at ~4 kt for about 20-25 min. Macrozooplankton was preserved in a 4% buffered formaldehyde seawater solution and identified to the lowest possible taxon. Densities were expressed as ind.1000 m^{-3}.

HIPPIES: Heard Island sampling, February 2004

Macrozooplankton were sampled from three locations to the east of Heard Island between 1 and 21 January 2004 aboard RV *Aurora Australis*, during the HIPPIES research program. Samples were collected with an RMT-8 with a notional mouth area of 8 m^2 and mesh size of 2 mm. The mesh size of the cod-end bag was 0.85 mm. The net was towed obliquely at a speed of ~2.5 kt, sampling three depth strata (0-100 m, 100-300 m and 300-600 m), taking ~30 minutes for each stratum. The net was equipped with a control and monitoring device manufactured at the Australian Antarctic Division (AAD) that provided real-time information on the depth of the net and allowed the net to be opened and closed on demand, at the bottom and top of the sampled depth stratum. The volume filtered for each haul of the RMT-8 was calculated from the tow distance as indicated by a General Oceanics flowmeter mounted in the mouth of the net and the effective mouth area of the net, calculated by the method of Pommeranz *et al*. (1983). A Falmouth Scientific Instruments (FSI) micro 3" CTD was placed on the net frame to measure depth, temperature and salinity data throughout the haul.

Samples were preserved in 10% buffered formaldehyde in seawater and returned to the laboratory where they were identified to the lowest possible taxon. For the purpose of this study, only abundance data from the upper 300 m were used, and expressed as ind.1000 m^{-3}.

SANAP sampling at the Prince Edward Islands, April 1997 and April 2003

SANAP macrozooplankton samples were collected using an RMT-8 with a mesh size of 4.5 mm and cod-end mesh size of 0.9 mm. The net was towed obliquely between 300 m and the surface at each station at a speed of ~2.5 kt for 20 to 25 minutes. The trawl was fitted with a universal underwater

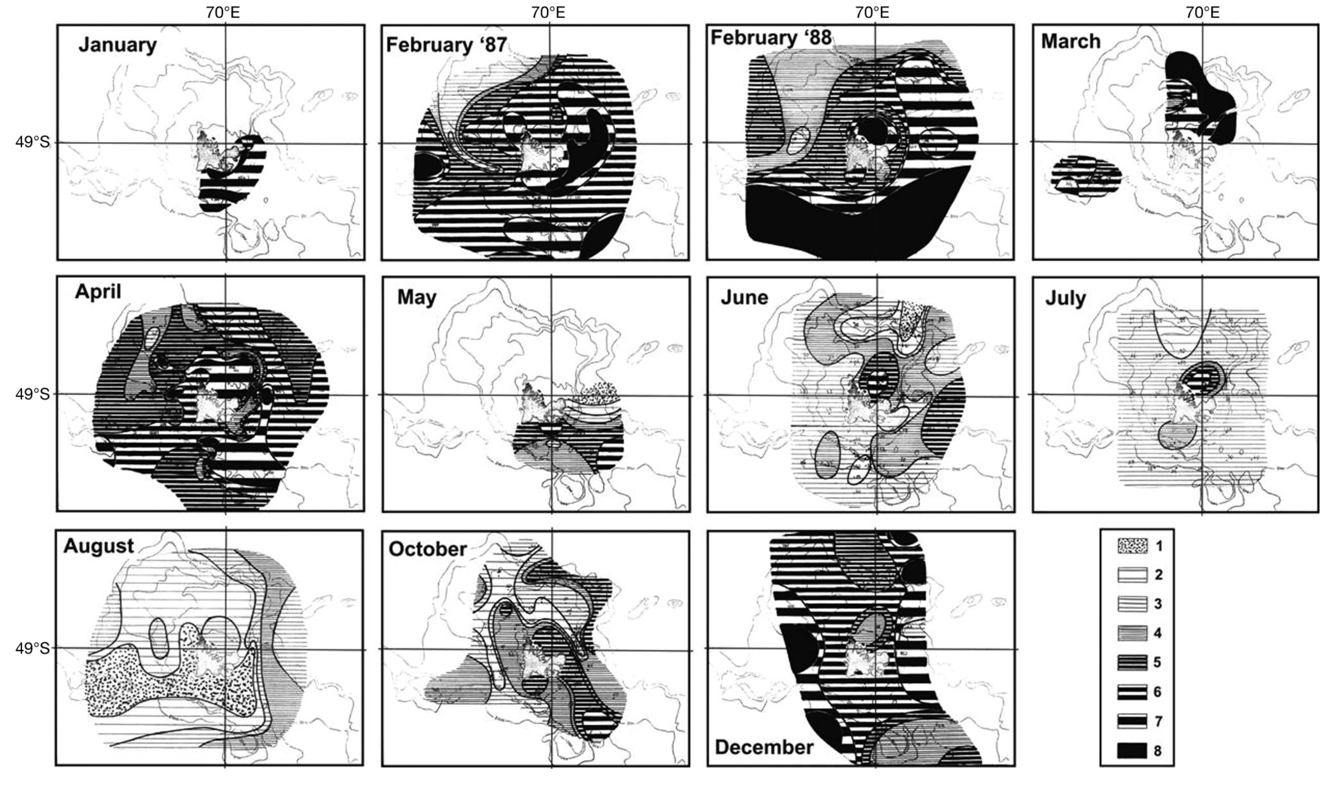


Figure 3. - Compilation of *ad hoc* seston surveys conducted during YugNIRO expeditions between 1980 and 1990 in the vicinity of the Kerguelen Islands. The surveys are compiled as a monthly composite highlighting intra-annual variability in seston abundance and its spatial distribution in the 0-100 m layer, for all months of the year except September and November. The February 1987 and February 1988 surveys are highlighted. 1: < 10; 2: 10-25; 3: 26-50; 4: 51-100; 5: 101-250; 6: 251-500; 7: 501-1000; and 8: > 1000 mgWW.m^{-3}.

unit (U3, Robertson *et al*., 1981) that continuously monitored depth and temperature. The volume filtered by the trawl was determined by multiplying the effective mouth area of the trawl by the distance travelled. This was calculated from the ship's speed and the duration of net opening. In calculating the volume filtered, the effect of towing speed was also taken into account (Roe *et al*., 1980). Samples were preserved in 6% buffered formalin and returned to the laboratory where the macrozooplankton were identified to the lowest possible taxon. Macrozooplankton abundance data were expressed as ind.1000 m^{-3}.

The SANAP samples used here come from two surveys aboard the MV *SA Agulhas*. The first (MIOS2), in April 1997, completed a grid of stations to the east and west of the Prince Edward Islands and is reported on by Pakhomov *et al*. (2000). The second (DEIMEC II), in April 2003, sampled the region south of the Prince Edward Islands to 54°S (Pakhomov *et al*. 2003), and is reported on in detail in Ansorge *et al*. (2010).

Biogeographic Analysis

For the purpose of the biogeographic analysis we reduced the data set to one comprised of only euphausiids. Euphausiids have one of the best resolved species distributions, and are excellent bio-indicators of different water masses (Kirkwood, 1982; Gibbons *et al*., 1999). The euphausiid abundance data (ind.1000 m^{-3}) from the February 1988 Melnikov's net survey, HIPPIES, MIOS 2 and DEIMEC II were collated into a station by species presence / absence matrix. Sorenson's index was then used to produce a station similarity matrix, and the stations subsequently clustered using group average sorting. SIMPER analysis was used to identify which species contributed most to each station group identified. All analyses were performed using Primer 6.

RESULTS

1987-1988 Seston data

A strong seasonal signal in the total seston within the 0-100 m layer was observed in the vicinity of the Kerguelen Islands (Figs 2 and 3), despite extreme patchiness in its spatial distribution (Fig. 3). The summer period, lasting from December through to April, appeared to be the most productive with average seston biomass varying between 305 and 1015 mgWW.m^{-3}. The highest seston biomass were observed from January to March, often exceeding 2 gWW.m^{-3}. It should be noted that seston surveys during both January and March covered a fraction of the area typically surveyed (Fig. 3) and may have distorted the annual cycle (Fig. 2). High biomass levels (1000 mgWW.m^{-3}) were observed both north (March) and south (February 1988) of the islands. Seston biomass was lowest during the winter months between May and October, and biomass appeared to be highest closer to the islands at this time (101-500 mgWW.m^{-3}).

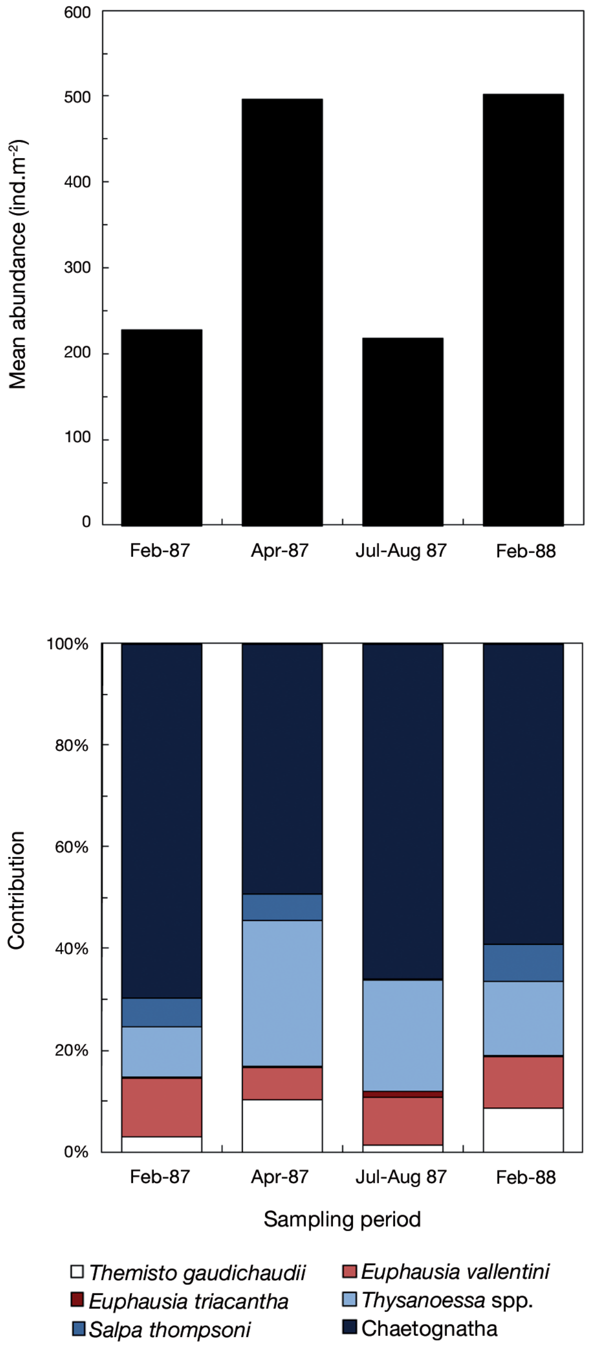


Figure 4. - Mean abundance and composition of six major macrozooplankton taxa in the top 500 m (or to the bottom) layer between February 1987 and February 1988.

A significant dip (t-test; $p < 0.05$) in mean seston values was observed for the combined February 1987 and February 1988 samples. Although February 1987 appeared to be unique in the 1987-1988 time series, February 1988 seston biomass on its own (740 ± 74 mgWW.m^{-3}) was lower (though not significantly; $p > 0.05$) than January and March. It is possible that the first seston peak was linked to the early summer phytoplankton bloom (Ivanchenko 1992), and the March peak associated with the peak in mesozooplankton biomass (Semelkina 1992, 1993).

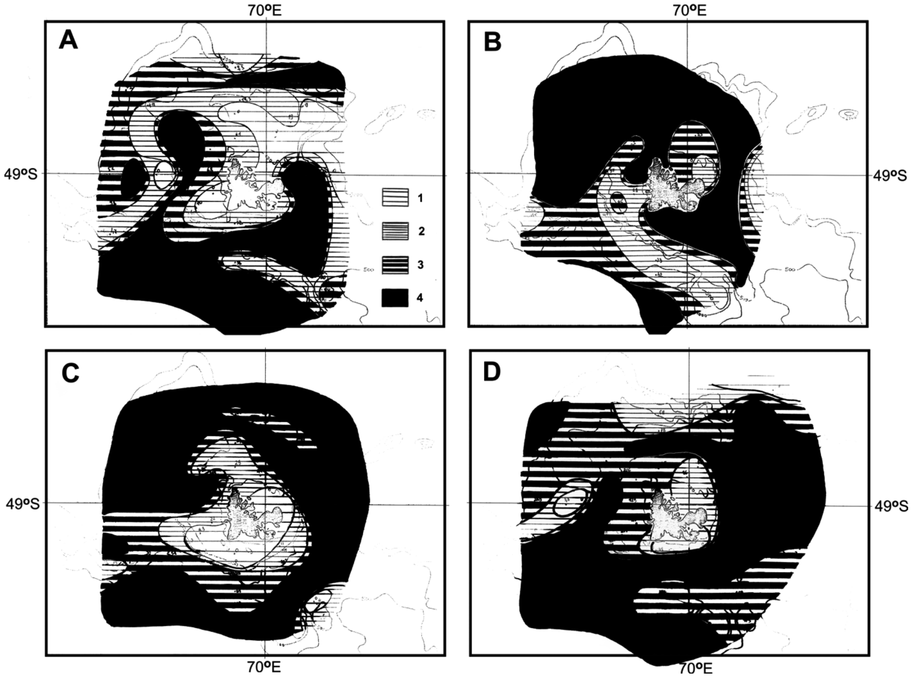


Figure 5. - Spatial distribution of chaetognaths in the top 500 m (or to the bottom) layer between February 1987 and February 1988. **A**: February 1987; **B**: April 1987; **C**: July-August 1987; **D**: February 1988. **1**: < 50; **2**: 50-100; **3**: 101-300; and **4**: > 300 ind.m^{-2}.

Seasonal cycle of principal macrozooplankton species (1987-1988)

Among the six major macrozooplankton taxa, chaetognaths were the most consistent and dominant group year-round, accounting in general for > 50% (range 49-70%) of the total abundance for the six macrozooplankton species considered here (Fig. 4). Their mean abundance ranged from 143 to 296 ind.m^{-2}. The spatial distribution pattern of chaetognaths was similar year around, with lower densities regularly observed near the islands and higher densities associated with the offshore waters (Fig. 5). Notably, chaetognath densities were substantially lower north and northeast of the islands in February 1987 compared to February 1988.

Thysanoessa spp. was the second most numerous macrozooplankton taxon, accounting for 10-29% of total abundance year around (Fig. 4). *Thysanoessa* spp. were most numerous (143 ind.m^{-2}) in April 1987 and lowest (22 ind.m^{-2}) in February 1987. This group was patchily distributed but, in general, the highest catches were found away from the islands with the exception of the northern shelf (Fig. 6).

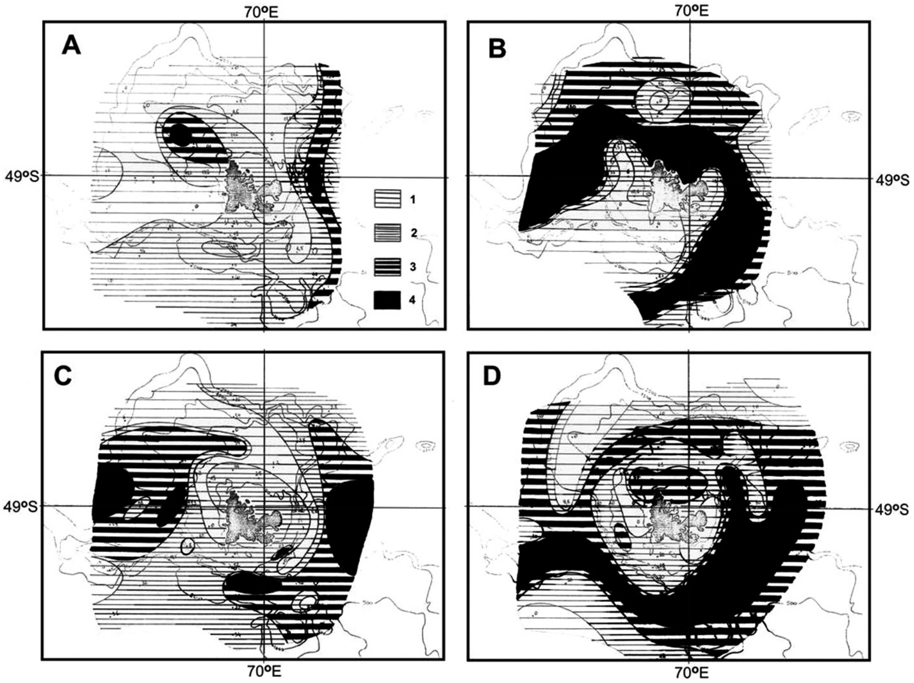


Figure 6. - Spatial distribution of *Thysanoessa* spp. in the top 500 m (or to the bottom) layer between February 1987 and February 1988. **A**: February 1987; **B**: April 1987; **C**: July-August 1987; **D**: February 1988. **1**: < 10; **2**: 10-50; **3**: 51-100; and **4**: > 100 ind.m^{-2}.

E. vallentini and *T. gaudichaudii* were of a similar numerical importance, accounting for 6-11% and 1-10% of total macrozooplankton abundance year-round respectively (Fig. 4). While both species were most numerous in February 1988 and April 1987, *T. gaudichaudii* showed very strong seasonality and inter-annual variability, being almost absent from samples in winter and ~6 fold less numerous in February 1987 compared to February 1988 samples (Figs 4 and 7). Spatially, *T. gaudichaudii* was most abundant over

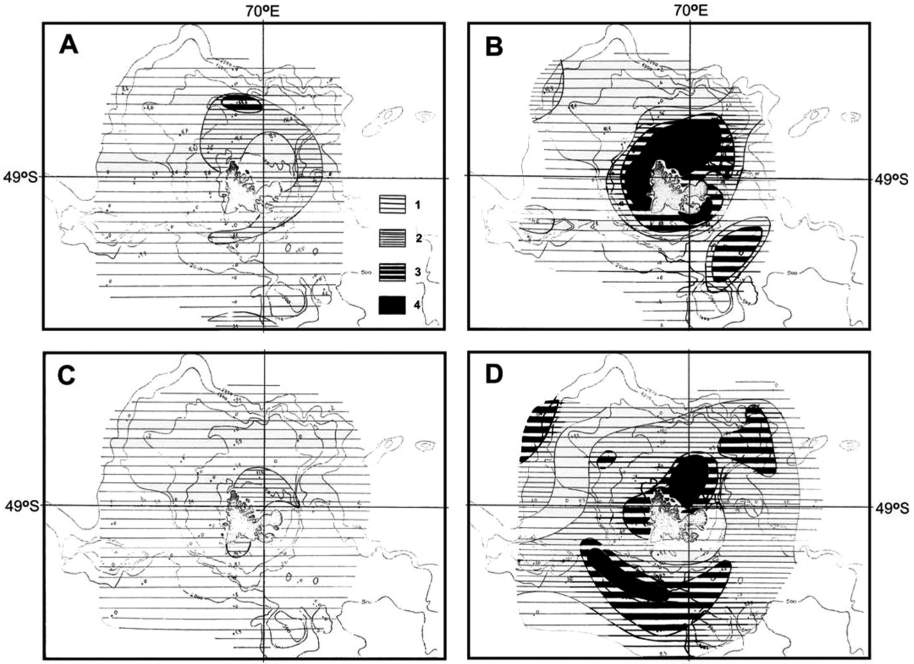


Figure 7. - Spatial distribution of *Themisto gaudichaudii* in the top 500 m (or to the bottom) layer between February 1987 and February 1988. **A**: February 1987; **B**: April 1987; **C**: July-August 1987; **D**: February 1988. **1**: < 10; **2**: 10-50; **3**: 51-100; and **4**: > 100 ind.m^{-2}

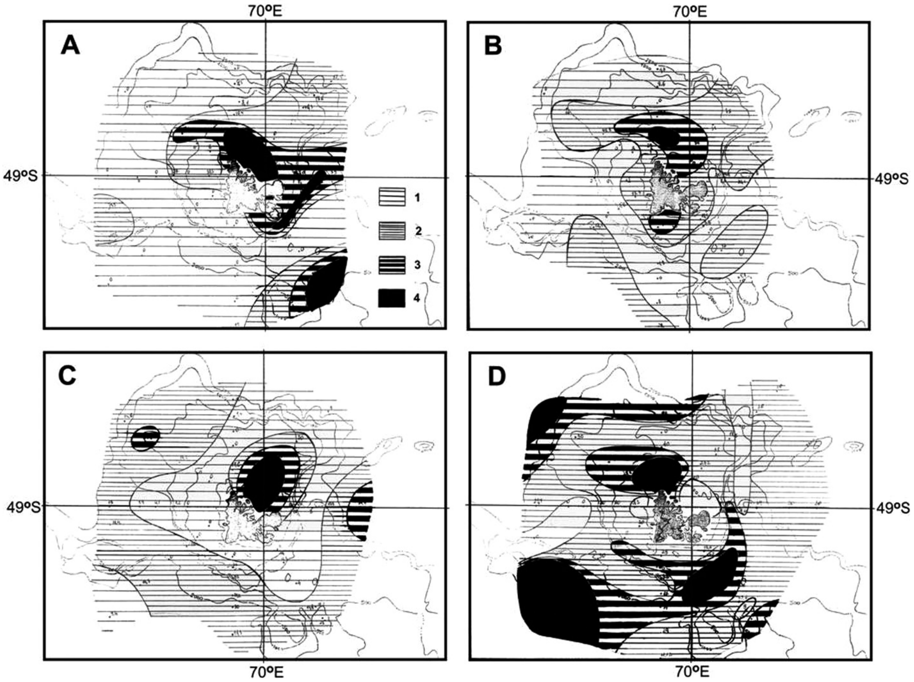


Figure 8. - Spatial distribution of *Euphausia vallentini* in the top 500 m (or to the bottom) layer between February 1987 and February 1988. **A**: February 1987; **B**: April 1987; **C**: July-August 1987; **D**: February 1988. **1**: < 10; **2**: 10-50; **3**: 51-100; and **4**: > 100 ind.m^{-2}.

the northern shelf of the islands and occasionally over the shelf to the south. Seasonal and inter-annual differences in *E. vallentini* abundance were modest and usually did not vary more than two-fold (Fig. 4). This euphausiid was most numerous over the northern shelf region of the Kerguelen Islands and over the shelf and shelf break north and south of the islands during the summer months (Fig. 8).

The tunicate *S. thompsoni* was almost absent from the samples during the winter months and was very patchily distributed for the rest of the year appearing in samples mainly south of 49°S west and east of the islands over the deep waters (Fig. 9). Its contribution varied between 0.1 and 7% of total macrozooplankton abundance (Fig. 4).

Inter-annual variability: February 1987 and 1988

Data on phytoplankton and mesozooplankton showed that plankton communities differed drastically between February 1987 and February 1988 (Ivanchenko, 1992; Semelkina, 1992), corresponding with different oceanographic conditions (Kljausov, 1990). In February 1987 a strong southward influx of warm modified sub-Antarctic and sub-Tropical waters was identified over the Kerguelen Plateau, extending as far as the southern shelf of the islands, associated with a southward shift of the SAF (Kljausov, 1990). Conversely, in February 1988 the "normal" oceanographic situation was encountered, with the PF passing to the north of the islands.

Ivanchenko (1992) found that the average phytoplankton biomass in the top 100 m was two-fold higher during February 1987 than in February 1988 (362 *vs* 185 mg.m^{-3}). During February 1987 large sub-Antarctic phytoplankton species (e.g., genera *Rhizosolenia*, *Chaetoceros*) dominated, while three species of subtropical dinoflagellates were recorded (Ivanchenko O.I., personal communication). During February 1988 small Antarctic phytoplankton species (genera *Nitzschia*, *Thalassiothrix*) were most numer-

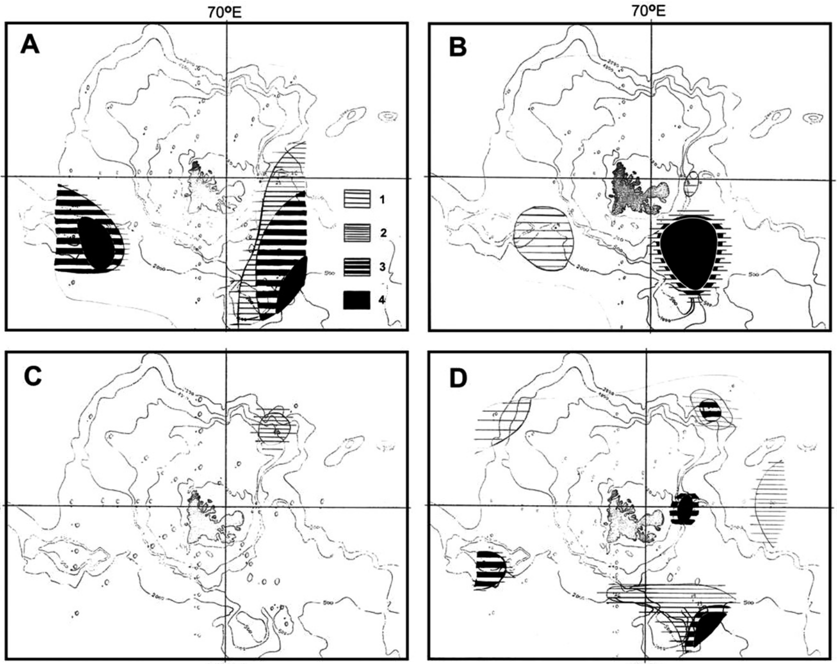


Figure 9. - Spatial distribution of *Salpa thompsoni* in the top 500 m (or to the bottom) layer between February 1987 and February 1988. **A**: February 1987; **B**: April 1987; **C**: July-August 1987; **D**: February 1988. **1**: < 10; **2**: 10-50; **3**: 51-100; and **4**: > 100 ind.m^{-2}

ous (Ivanchenko, 1992).

Although phytoplankton biomass was higher in February 1987, seston biomass was on average lower compared to February 1988 (Fig. 3). Mesozooplankton (mainly copepods, and particularly *Drepanopus pectinatus* Brady 1883) biomass was low during February 1987, with average values similar to winter levels, and population development (copepodite stage composition) appeared to be depressed (Semelkina, 1992). Our macrozooplankton data showed a similar pattern to mesozooplankton with February 1987 densities being similar to winter levels. During February 1987, seventeen subtropical / sub-Antarctic copepod species (e.g., adult stages of *Calanus minor* Claus 1863 and *Undinula vulgaris* Dana 1849 (Semelkina, 1993), and several macrozooplankton species (e.g., *Euphausia spinifera* G.O. Sars 1883, *Thysanoessa gregaria* G.O. Sars 1883, this study), were recorded to the south of the Kerguelen Islands. True Antarctic species such as *Clio sulcata* Pfeffer 1879 and *Thysanoessa macrura* G.O. Sars 1883 were restricted to a few of the southernmost stations during February 1987. A high frequency of subtropical indicator species, both north and south of the Kerguelen Islands, was also observed amongst the macrozooplankton in February 1987 (Fig. 10). The frequency of occurrence of Antarctic species was only slightly higher in February 1988, but what was remarkable about this survey was the low frequency of occurrence of subtropical / sub-Antarctic indicator species to the north of the Kerguelen Islands (Fig. 10).

Regional biogeography and community structure

As a baseline for comparison, we have presented the generalised frontal positions of Belkin and Gordon (1996) in figure 11. Three station groupings were identified from the cluster analysis of euphausiid presence/absence data (Fig. 11). Group 1 comprised MIOS 2 (April 1997) stations from the vicinity of the PEI and the northernmost DEIMEC II stations. This group was characterised by species typical of the sub-Antarctic Zone (SAZ) and Polar Frontal Zone (PFZ), including *Euphausia longirostris* Hansen 1908, *E. similis*

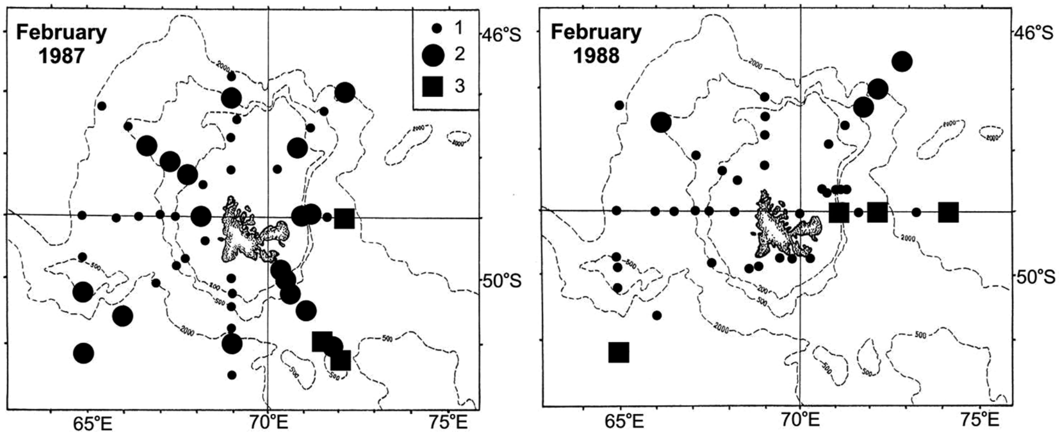
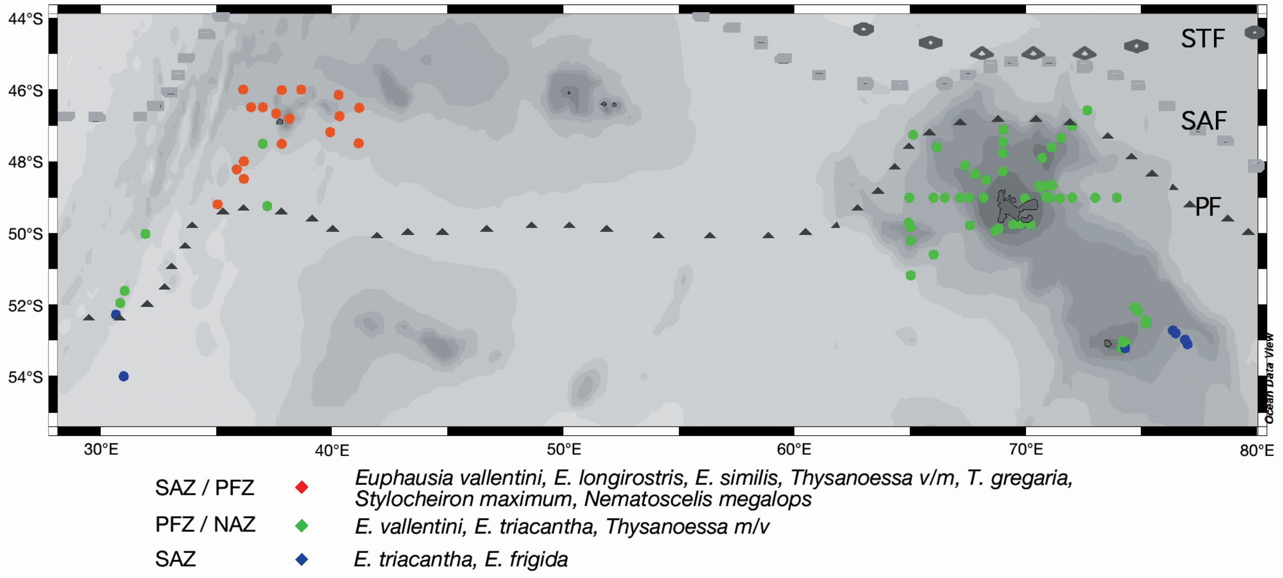


Figure 10. - Presence/absence of subtropical and Antarctic macrozooplankton species during February 1987 and February 1988. 1: sampling stations; 2: stations where subtropical indicator species were found; 3: stations where Antarctic indicator species were found.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Ocean Data View
SAZ / PFZ ◆ *Euphausia vallentini, E. longirostris, E. similis, Thysanoessa v/m, T. gregaria, Stylocheiron maximum, Nematoscelis megalops*
PFZ / NAZ ◆ *E. vallentini, E. triacantha, Thysanoessa m/v*
SAZ ◆ *E. triacantha, E. frigida*

Figure 11. - The distribution of sample groupings, indicated by different colour markers, resulting from the cluster analysis of euphausiid presence/absence data. The stations comprise the macrozooplankton samples from the MIOS 2 (1997), DEIMEC II (2003), YugNIRO (February 1988) and HIPPIES (2004) surveys. The positions of the Sub-Tropical Front (STF), Sub-Antarctic Front (SAF) and Polar Front (PF) are indicated following Belkin and Gordon (1996). Below the map the species contributing most to within cluster similarity are indicated, identified by Simper analysis (Primer 6), and the zones that they are indicators for: SAZ – Sub-Antarctic Zone, between the STF and SAF; PFZ – Polar Frontal Zone, between the SAF and PF; northern-AZ – northern Antarctic zone; southern-AZ – Southern Antarctic Zone.

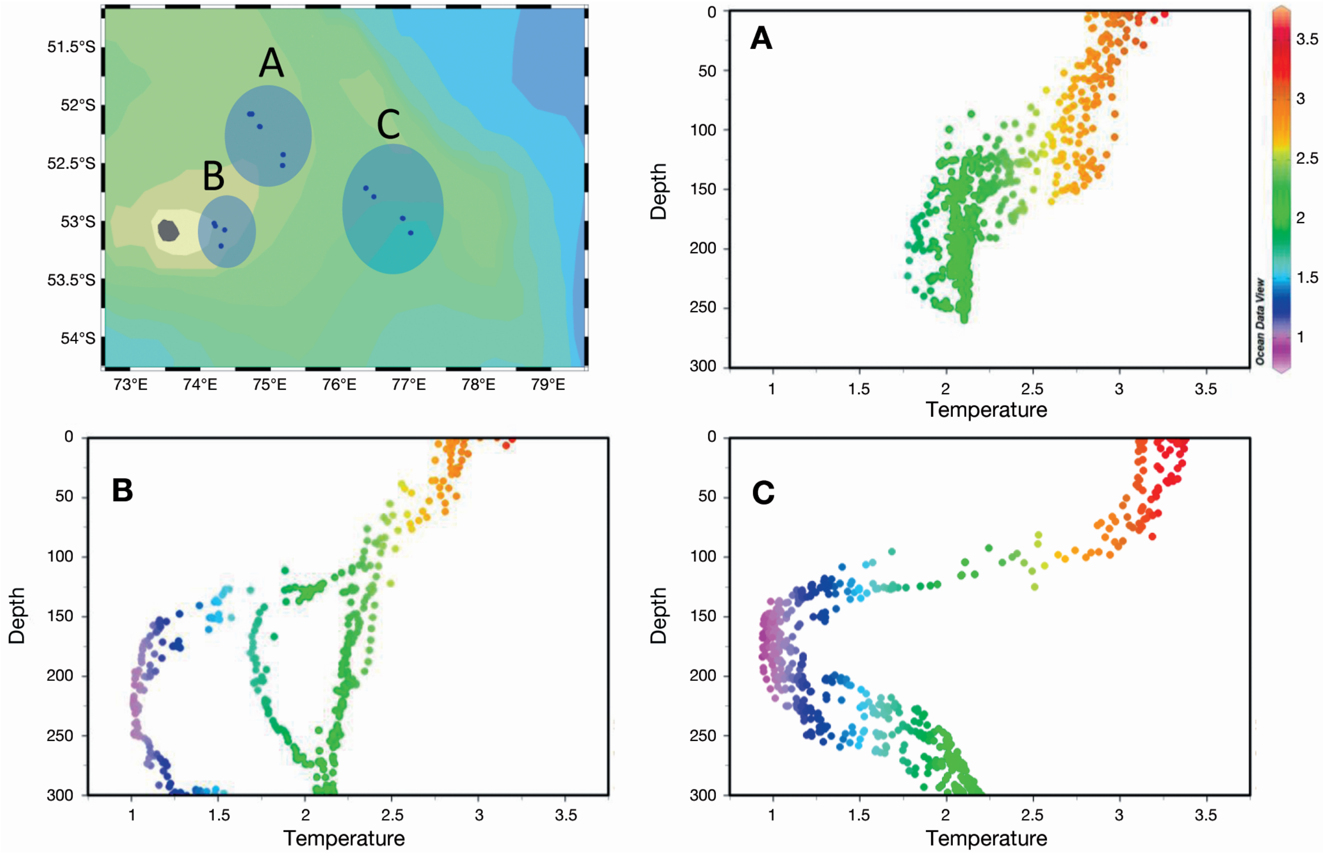

Figure 12. - Temperature (°C) profiles of macrozooplankton RMT-8 net hauls, grouped for the three research areas (A, B, C) during the HIPPIES sampling program.

G.O. Sars 1883, *E. vallentini*, *Thysanoessa* spp., *T. gregaria*, *Stylocheiron maximum* Hansen 1908, and *Nematoscelis megalops* G.O. Sars 1883. During MIOS 2 the PF demonstrated extensive meandering and was encountered further north than the average positions of Belkin and Gordon (1996), to 48°S in the east and west of the survey area (Froneman *et al*., 1999; Pakhomov *et al*., 2000). However, the majority of samples were located within the PFZ, between the SAF in the north and PF in the south. During DEIMEC II the PF was found to meander between 48 and 52°S and the northern samples of Group 1 were therefore largely within the PFZ (Ansorge *et al*., 2010).

Group 2 comprised stations from the north and central part of the DEIMEC II, all of the YugNIRO samples (February 1988) from the vicinity of Kerguelen Island, the northernmost HIPPIES samples (Area A, Fig. 12) and three of the western HIPPIES samples (Area B, Fig. 12) in the lee of Heard Island (Fig. 11). Group 2 was characterised by the PFZ and northern-AZ species, *E. vallentini*, *E. triacantha* and *Thysanoessa* spp.. As described above, during the February 1988 survey, the PF passed to the north of Kerguelen Island. The distributions of *E. vallentini* and *E. triacantha* as sampled by Melnikov's net during the YugNIRO February 1988 macrozooplankton survey are presented in Figure 13 to complement the data from the Juday net surveys conducted in 1987 and 1988 (Figs 5-9). The distribution of *E. vallentini* measured by the Melnikov's net was similar to that determined using the Juday net (Figs 8 and 13), with abundance being highest in close proximity to Kerguelen Island and lowest to the south. *E. triacantha*, not presented for Juday net samples, was primarily distributed to the south of the Kerguelen but was also found in low densities to the north, giving good support for the PF passing to the north of the islands at this time, as this is a species is typically not found in the PFZ. The Area A and three Area B samples (Fig. 12) in Group 2 were all characterised by relatively warm water (> 2°C) considered to have a northern origin (van Wijk *et al*., 2010). The high frequency of occurrence of *E. vallentini* suggested a strong PFZ influence.

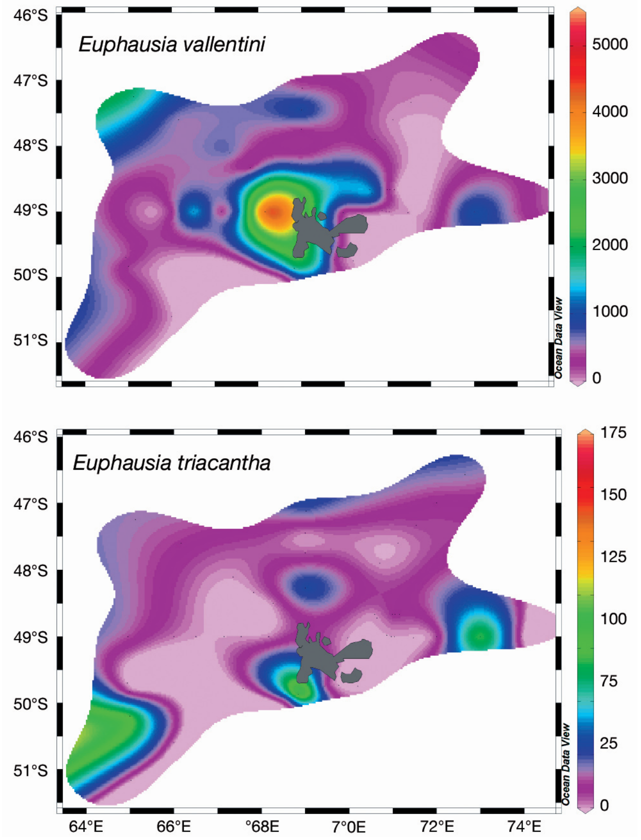

Figure 13. - Abundance distribution of *Euphausia vallentini* and *E. triacantha* in the vicinity of the Kerguelen Islands, as sampled by a Melnikov's net during the YugNIRO February 1988 macrozooplankton survey.

Group 3 comprised the eastern HIPPIES (Area C, Fig. 12) and two of the Area B samples, as well as the two southernmost DEIMEC II samples (Fig. 11). This group was characterised by the northern-AZ species *E. triacantha* and the southern-AZ species *E. frigida* Hansen 1911. The Heard Island samples in Group 3 were all from deep waters (> 100 m) colder than 2°C characteristic of water south of the PF and within the AZ (van Wijk *et al*., 2010). The euphausiid distribution between the Heard Island stations therefore closely matched the water mass properties.

Regionally, substantial differences were apparent in both macrozooplankton abundance and composition (Fig. 14). Total macrozooplankton abundance was comparable between the 1988 Kerguelen samples and the 2004 Heard Island sample, but both were three orders of magnitude higher than levels recorded to the west of the Kerguelen plateau, including the vicinity of the Prince Edward Islands. At Heard Island, euphausiids and chaetognaths were equally dominant and the major components of the macrozooplankton community, contributing 45% and 44% to total macrozooplankton abundance respectively. Euphausiids (63%) alone dominated the vicinity of Kerguelen and the Prince Edward Islands, while chaetognaths and amphipods were also important components of the macrozooplankton (7-20%). The DEIMEC II samples from south of the Prince Edward Islands were dominated by salps (73%).

DISCUSSION

The combined YugNIRO, MIOS 2, DEIMEC II and HIPPIES data sets provide insights into the biogeography of the Indian Ocean sub-Antarctic islands on a number of different spatial and temporal scales. Results from individual meso-scale oceanographic surveys show that biogeography is dominated by spatial variability related to the distribution

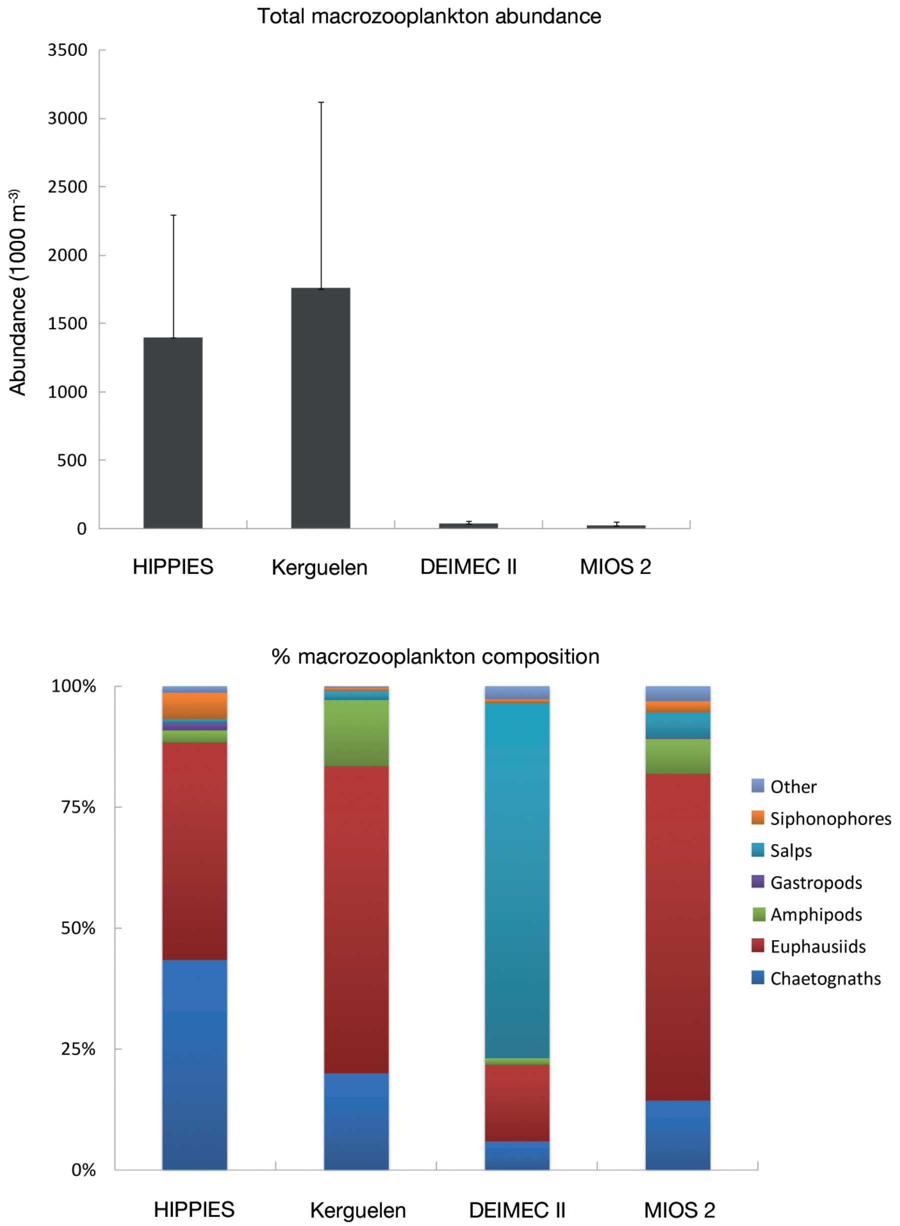

Figure 14. - Average abundance and macrozooplankton composition for the YugNIRO (Kerguelen), MIOS 2, DEIMEC II and HIPPIES surveys.

of water masses through fronts and eddies. The spatial complexity of water mass distributions at any one time is highly variable in the Southern Ocean, with greater complexity stimulated in regions of shallow or interrupted topography. The south-west Indian Ridge upstream of the PEI, and the PEI themselves, cause an unusually high degree of mesoscale variability and a high frequency occurrence of eddies (Ansorge *et al*., 2010). This is reflected by the composition of biota within the PFZ in the vicinity of the PEIs comprising a mix of SAZ, PFZ and AZ taxa. Oceanographic data collected in the vicinity of the northern Kerguelen Plateau during the YugNIRO surveys indicated a similarly dynamic region with extensive frontal meandering and water retention through eddy formation in the lee of the islands (Murail *et al*., 1977, Kljausov, 1990, Lanin *et al*., 1990). This variability is clearly evident in the distribution of species and total abundance levels, and seston biomass in the YugNIRO contour plots for the region.

Inter-survey comparisons, such as the seasonal YugNIRO sampling in 1987 and 1988, are dominated by the seasonal cycle of abundance and between-survey variation in oceanographic structure, which in this instance also had an inter-annual component. The spatial distribution of zooplankton varied substantially from one survey to the next, most likely due to the highly dynamic water mass distributions. High concentrations of crustaceans, both euphausiids and hyperiids (*T. gaudichaudii*), were found consistently over the northern and north-western shelf of the Kerguelen Islands. These concentrations persisted year around and were most likely associated with the quasi-stationary mesoscale oceanographic features in the area. *T. gaudichaudii* is one of the most important near shore prey items for top predators (Bocher *et al.*, 2001). *T. gaudichaudii* was typically less abundant in offshore waters, however, euphausiids were relatively abundant here and appeared to show enhanced concentrations in the shelf-break and slope regions.

Between-survey spatial variability was overlaid by a strong seasonal cycle of abundance, characterised by a summer peak (December to April) and winter low (May to October). Notably, seston biomass during the winter months was highest close to the Kerguelen Islands. At still larger temporal scales, the seasonal cycle observed at the Kerguelen Islands was affected by inter-annual variation due to the shift of the PF from south of the islands in February 1987 to north of the islands in February 1988. The 1987 situation, considered abnormal at that time (Semelkina, 1992), was associated with an influx of sub-Antarctic and sub-tropical zooplankton species, reaching the southern Kerguelen Island shelf, as well as reduced February 1987 zooplankton abundance levels (Pakhomov, 1995).

Using euphausiid data, three distinct macrozooplankton groups were identified across the greater Kerguelen Plateau–PEI region. These comprised a mixed SAZ/PFZ community, a mixed PFZ/northern-AZ community, and a southern-AZ community. The SAZ/PFZ community was most diverse and included species with sub-tropical origins such as *S. maximum* and *N. megalops* (Kirkwood, 1982). Given the substantial time difference between the surveys used in this analysis, the observed biogeographic patterns need to be considered in the light of long-term oceanographic change. The February 1988 macrozooplankton data, particularly the occurrence of *E. triacantha* north of the islands, provide strong support for the passage of the PF to the north of the Kerguelen Islands, as suggested by numerous authors (Gamberoni *et al.*, 1982; Orsi *et al.*, 1995; Belkin and Gordon, 1996). Conversely, the occurrence of PFZ species in the vicinity of Heard Island, and a high abundance of *E. vallentini*, indicates the southward transport of PFZ waters over the northern Kerguelen Plateau during summer 2003/2004 (van Wijk *et al.*, 2010), and lends biological support for the N-PF passing through the Fawn Trough in 2004 (Sokolov and Rintoul, 2009).

The shift in the N-PF from passing north of the Kerguelen Islands between 1992 and 2003 to passing through the Fawn Trough between 2004 and 2007 (a southward shift of 10° latitude), identified using satellite altimetry data, suggests a long term trend of directional oceanographic change (Sokolov and Rintoul, 2009). However, the contrasting oceanographic conditions between early 1987 and 1988, highlighted by the YugNIRO surveys, indicate that an alternation between a north and south passage of the PF with respect to the Kerguelen Islands may be a natural feature of this ecosystem's variability. Whether a trend or not, the shift from one condition to the other has a profound ecosystem level impact. In 1987, these impacts included increased phytoplankton biomass, suppressed zooplankton development and correspondingly lower abundance, and a substantial shift in species composition. The latter potentially has an important bearing on ecosystem function, as evidenced by differences in the biology of the PFZ euphausiid *E. vallentini* and the northern-AZ species *E. triacantha*, two species that were strongly affected by shifts in the PF in this study. For example, a predominance of the herbivorous omnivore *E. vallentini* will result in a more efficient transfer of primary production to upper trophic levels than a predominance of the carnivorous omnivore *E. triacantha*. In addition, the quality of these two species as prey may differ substantially due to their different trophic levels, while their availability to predators differs due to their different depth distributions (Bost *et al.*, 2002). The species *E. triacantha* is a mesopelagic migrator while *E. vallentini* is an epipelagic species. These differences were clearly evident in stratified net hauls conducted during the HIPPIES survey at Heard Island (Williams *et al.*, unpublished data).

An additional observation from our data set for the greater Kerguelen Plateau-PEI region was the substantial regional differences in macrozooplankton abundance and composition. The gear used to sample the macrozooplankton may have played a role in this. Although the same gears (RMT-8) were used for the MIOS 2, DEIMEC II and HIPPIES surveys, the mesh size of the HIPPIES nets was half that of the latter, although the cod end mesh sizes were almost identical. Conversely, the small mouth area of the Melnikov's net used during the February 1988 survey may have undersampled components of the macrozooplankton, which due to their size and mobility are more capable of net avoidance. However, the same gear was used for the MIOS 2 and DEIMEC II surveys, and these data show that macrozooplankton densities in the vicinity of the PEI were similar to the Permanently Open Ocean Zone (POOZ) to the south. Overall, therefore, it does appear that from a top predator perspective the Kerguelen plateau is a substantially more productive region than that in the vicinity of the PEI. This is perhaps not surprising given the large seasonal phytoplankton biomass accumulation that occurs in the former region (Blain *et al.*, 2007).

The high productivity of the Kerguelen Plateau appears to be largely driven by hydrographic processes, including the upwelling of iron and other nutrients from deep water (Blain *et al.*, 2007), and water retention over the shallow shelf (Park *et al.*, 2008a; Park *et al.*, 2008b). In view of the importance of local hydrodynamics, changes in the oceanographic environment on the Kerguelen Plateau may have a significant impact on productivity (Sokolov and Rintoul, 2009). Our data show that shifts in the frontal positions correspond with dramatic changes in the composition and development of the entire plankton community in the vicinity of the islands. This may have important direct implications for the top predators on the island as well as indirectly via the abundance of mesopelagic and benthopelagic fish which provide significant forage for many seabirds and seals, and also shelf benthos. These impacts may occur in both the short term (e.g., mortality and recruitment success) and long-term (e.g., population trends). Indeed, fisheries data from the 1980s found a negative relationship between the southward extent of the SAF and PFZ and catches of the benthopelagic fish species *Champsocephalus gunnari* Lönnberg, 1905(Lanin *et al*., 1990), while long term changes in the populations of predator species have already been demonstrated, for example the decline in gentoo penguins observed between 1987 and 2004 (Lescroel and Bost, 2006).

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